GRIZZLY AND BLACK BEAR DENSITIES IN INTERIOR BRITISH COLUMBIA

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Canadian Forest Products Ltd. 5162 Northwood Pulpmill Road Box 9000, Prince George, BC, V2L 4W2

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B.C. Ministry of Water, Land, and Air Protection Fish and Wildlife Branch, Omineca Subregion 1011 4th Ave., Prince George, BC, V2L 3H9

Prepared by:

G. Mowat¹, K. G. Poole¹, D. R. Seip², D. C. Heard³, R. Smith⁴, and D. W. Paetkau⁵

¹Aurora Wildlife Research RR 1, Site 14, Comp 8 Crescent Valley, BC, V0G 1H0 Tel: (250) 359-7699; e-mail: gmowat@telus.net

²British Columbia Ministry of Forests, Prince George, BC

³British Columbia Ministry of Water, Land, and Air Protection, Prince George, BC

⁴Lheidli T'enneh Band, Prince George, BC

⁵Wildlife Genetics International, Nelson, BC

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ABSTRACT

We used genetic identification of individuals and mark-recapture modeling to estimate bear (*Ursus*) population size in both a mountainous and interior plateau environment in central eastern British Columbia. We sampled 591 sites within a 9,452-km² study area during June and July 2000 and detected grizzly bears (*Ursus arctos*) at 199 sites and black bears (*U. americanus*) at 316 sites. We identified 326 different grizzly bears using microsatellite profiling; there were more females than males in the sample (35M:65F). After correcting for the effects of closure bias, we estimated density to be 12 grizzly bears/1,000 km² (95% confidence interval [CI] 7–28) on the plateau and 49/1,000 km² (CI 43–59) in the mountains. These densities are considerably higher than those predicted by the habitat-based extrapolation method used for grizzly bear management in British Columbia. The incorporation of hunter harvest impacts to population size caused the greatest decline, and therefore discrepancy, in numbers between the habitat-based extrapolation and the DNA-based estimate.

We also sampled grizzly bears along 47 km of stream during August 2000 when Chinook salmon (*Oncorhynchus tshawytcha*) were in the streams. We detected 15 different grizzly bears at the 10 sites we sampled, and estimated there were 21 grizzly bears (CI 16–44) present along these streams during the 2 weeks we sampled. Eleven of the 15 bears detected along the salmon streams had been previously detected during spring sampling and the movement distance detected for most bears was within the range expected given home range sizes in this area. However, 2 male bears made what appeared to be extraterritorial movements to the salmon streams (35 and 48 km). These streams historically have modest salmon runs, which highlight the importance of salmon to interior grizzly bears.

Grizzly bear densities are higher on the west slopes of the Rocky Mountains, including the front ranges such as the Selkirk and Purcell Mountains, than on the east slopes of the Rockies and in boreal and sub-plains environments. Subpopulations in the Rocky Mountain west slopes that are discontinuous with surrounding populations have lower landscape scale density than populations further north.

Black bear densities were 270 bears/1,000 km² (CI 173–458) on the plateau and 100/1,000 km² (CI 55-210) in the mountains. Spatial patterns in black bear densities appear to be opposite that of grizzly bears, with the highest densities occurring in boreal and sub-boreal plains environments and lower densities in mountainous environments. This observation may be more due to competition with grizzly bears than differences in habitat productivity.

DNA survey methods are expensive; thus, there will likely always be a need to use habitat-based extrapolations to predict bear abundance across broad areas. The Fuhr-Demarchi method as used now needs to be modified so that it is objective, repeatable and testable. We suggest that managers should use DNA-derived population estimates in various regions as benchmarks to calibrate the Fuhr-Demarchi method. Within the Parsnip/Herrick study area, our analysis suggests that current grizzly bear harvest levels are only sustainable in the Hart Ranges. Because salmon appear to be an important food source for grizzly bears in the upper Fraser River basin region, consideration should be given to retaining access to all salmon streams for bears during resource planning.

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INTRODUCTION

The conservation of grizzly bears (*Ursus arctos*) in British Columbia is a high profile wildlife management issue at the international, national, provincial and local level. The issue encompasses both concern about land use practices, and also the impact of hunting and other human caused mortality. Developing and evaluating conservation measures are made more difficult by the lack of agreement on how many grizzlies occur in different areas. There is much less conservation concern for black bear (*U. americanus*) populations in British Columbia, although the species is harvested in large numbers and no empirically derived estimates of abundance exists for the species in the province.

We required knowledge of grizzly bear distribution and abundance as part of ongoing research to help us interpret differences in bear habitat use and home range size (Ciarniello et al. 2001) between the McGregor Plateau and Nechako Lowlands, an area where logging activities were widespread, and the Hart Ranges, a mountainous area largely without roads and few industrial impacts (Ciarniello et al. in press). We also wanted to investigate the impact of a salmon run on both black and grizzly bear movements and density within part of the area. Population estimates would also aid in evaluating hunting management for both species. The objective of this study was to estimate population density of grizzly and black bears in 2 interior British Columbia ecosystems. We also wanted to compare our grizzly bear estimates to figures derived from habitat-based extrapolations prescribed for use in grizzly bear management by the British Columbia Wildlife Branch (Fuhr and Demarchi 1990, Ministry of Environment, Lands and Parks 1999) and, to other estimates of abundance for ecosystems in and around the Rocky Mountains.

STUDY AREA

The centre of our 9,452-km² study area was 110 km northeast of Prince George, British Columbia (Fig 1). The study area was divided into a northern (Parsnip) and southern (Herrick) area during fieldwork, and into the Fraser Basin ecoregion (hereafter plateau) and Hart Ranges ecosection (hereafter mountains) areas for analysis. We divided the study area for analysis because previous research indicated that grizzly bear home range sizes differed between those 2 biophysical zones, and there was limited movement of radiocollared bears between them (Ciarniello et al. 2001). The plateau portion of the study area included the Nechako Lowlands and McGregor Plateau ecosections and the mountainous portion was in the Central Canadian Rocky Mountain ecoregion. The dividing line between these distinct topographical areas was the border between the McGregor Plateau and Hart Ranges ecosections (Fig. 1, Demarchi et al. 1990:100). The 3,016-km² plateau area extended west from the bottom of the steep slopes on the east side of the Parsnip River. Elevations on the plateau ranged from about 800 to 1,100 m. The 6,436-km² Hart Ranges area extended to the east and southeast where elevations ranged from valley bottoms at about 800 m to peaks at 2,700 m.

The Parsnip area (6,168 km²) encompassed the Parsnip River and its tributaries, including the Missinka, Hominka, Table, Anzac and Chuchinka drainages, but also extended into the Sukunka River drainage to the east and across the interior plateau to the Crooked River drainage in the west. This area was in the Arctic watershed and consequently bears did not have local access to spawning salmon (*Oncorhynchus tshawytcha*). The Herrick area (3,284 km²) encompassed the Herrick Creek watershed and parts of the McGregor River drainage, including the James, Fontoniko, Spakwaniko, Framstead, Muller, Ovington, Gleason, Hedrick, and McCullagh creeks. Those drainages were in the Pacific watershed, and hence have fall salmon spawning runs. The Herrick Creek chinook salmon are a component of the early-summer Fraser River stock, which enters the lower portions of the Fraser River from April–July annually. Spawning fish reach natal streams in mid-August or September and spawn in the main stem of Herrick Creek and in James, Fontoniko, Ice and Spakwaniko creeks. Total numbers of spawning adults enumerated within Herrick Creek and associated tributaries have ranged from approximately 500 to 4,000 fish annually. Six hundred and seventy-nine fish were counted in fall 2000

and the run size was estimated at approximately 2,000 to 2,500 fish (B. Toth, Lheidli T'enneh Band, Prince George, unpublished data). Herrick Creek falls within the Traditional Territory of the Lheidli T'enneh Band, and the Parsnip area is within the Traditional Territory of the McLeod Lake Band. Small portions of Monkman Provincial Park, on the east side of the continental divide, were included in the Herrick study area, and Kakwa Provincial Park borders the study area to the southeast.



Figure 1. Parsnip/Herrick bear DNA inventory study area and site locations, 2000. Sites that detected grizzly bears are shown in solid circles, with proportionately larger circles depicting sites with the number of individuals detected (1–8 bears). Sites that did not detect grizzly bears are shown in open circles. The irregular line along the Parsnip River shows the approximate boundary between the plateau and mountains. The height of land between the Pacific and Arctic drainages of the Hart Ranges is shown running west of Monkman Provincial Park.

The most westerly portion of the plateau occurred in the SBSmk1 (Mossvale Moist Cool Sub-Boreal Spruce) biogeoclimatic variant, but the majority of the plateau was in the SBSwk1 (Willow Wet Cool) variant (Meidinger and Pojar 1991). In the mountains, the valley bottoms west of the continental divide occurred in the SBSvk (Very Wet Cool) subzone, with a small amount of ICHwk2 (Interior Cedar Hemlock Quesnel Wet Cool) and ICHvk2 (Slim Very Wet Cool) in the southern Herrick area along the McGregor River drainage. East of the continental divide, the valley bottoms were in the SBSwk2 (Finlay-Peace Wet Cool) biogeoclimatic variant. Two variants of the ESSF zone occurred in the mountains above the SBS zone. The lower elevation forests within the ESSF were typed as ESSFwk2 (Misinchinka Wet Cool Engelmann Spruce-Subalpine Fir), whereas the upper elevations of the ESSF were in the ESSFwc3 (Cariboo Wet Cold Engelmann Spruce-Subalpine Fir). The Alpine Tundra (AT) biogeoclimatic zone occurred above the ESSF beginning at about 1,400 to 1,550 m elevation.

Mean January and July temperatures in the plateau are -15° C and 16° C, respectively. The area receives roughly 73–141 cm of precipitation annually, with greater precipitation in the eastern (mountainous) portions of the study area (Reynolds 1989). Mean annual snowfall increases from about 300 cm in the plateau, up to 800 cm in the mountains. Total precipitation for June and July of 2000 was approximately 55% higher than the 9 to 11-year average (Ministry of Forests automated fire weather stations at the Table River [elevation 760 m] and McGregor River [elevation 975 m]).

The plateau portion of the study area primarily supported spruce (*Picea engelmannii* x glauca)– subalpine fir (*Abies lasiocarpa*) forests with a component of lodgepole pine (*Pinus contorta*) and trembling aspen (*Populus tremuloides*). Pine-dominated forests occurred on drier sites. The plateau has experienced extensive industrial development and contained a major highway (Highway 97) and a network of forest roads. The area contained 1 small community with 2 sawmills (Bear Lake), and 2 major logging camps (Anzac and Arctic). A substantial proportion of the plateau forests had been logged over the past 30 years and supported new and regenerating cutblocks.

In the mountainous portion of the study area, lower elevation forests were dominated by sprucesubalpine fir stands with scattered patches of lodgepole pine. The proportion of subalpine fir increased with elevation until it dominated upper elevation stands. Avalanche chutes were numerous and supported shrub-forb fields dominated by alder (*Alnus* spp.) at lower elevations, and lush forb meadows in subalpine areas. Large avalanche chutes measuring in the square kilometres were common. Rolling meadows and basins dominated by yellow glacier lily (*Erythronium grandiflorum*), Indian hellebore (*Veratrum viride*), false Solomon's-seal (*Smilacina racemosa*), and *Vaccinium* were common in the subalpine. Higher elevations contained a combination of barren rock, ice or alpine tundra communities.

The mountainous area had experienced much less industrial development than the plateau, although all major and some minor watersheds had logging roads along at least part of the valley bottom. Logging was generally at lower elevations and varied greatly in extent among drainages. Some higher elevation sites were logged using helicopter access; however, most upper elevations and the back ends of most watersheds were undeveloped wilderness. There was 1 major logging camp in the mountains (Herrick). Much of the logging development in the Herrick area had occurred since the construction of the Herrick Forest Service Road in 1996. The Table River valley contained the BCR railway line that passes through a tunnel to the Sukunka River valley on the eastern side of the Rockies, which was built in the 1970's to haul coal south from Tumbler Ridge.

The presence and intensity of recreational use varied seasonally and throughout the study area, and included hunting, fishing, camping, and all-terrain vehicle use. Spring and fall grizzly bear hunting was permitted, and was controlled by quota. Hunters were encouraged to shoot males; the shooting of females accompanied by young was prohibited. Black bears were hunted during spring and fall with a bag limit of 2 per hunter. The spring bear hunting season for both species during 2000 extended until 15 June and hence overlapped with the first 2 weeks of our fieldwork.

METHODS

Survey design

Following methods outlined in Woods et al. (1999), Mowat and Strobeck (2000), and Poole et al. (2001), we used a systematic grid design to distribute hair capture sampling effort across the study area. We selected an 8 x 8 km cell size (64 km^2), which was a trade-off between the desire to have cells as small as the smallest likely home range for that area (Ciarniello et al. 2001) and as large as possible to minimize costs. We selected study area boundaries to maximize geographic closure (White et al. 1982) based on movements observed from radiocollared grizzly bears (Ciarniello et al. 2001). We recognise that there were no real physical or behavioural barriers to movement along the study area boundary, except for a relatively small amount of glacier in the south (Fig. 1).

We divided the study area into 148 cells. Irregular shaped cells $<32 \text{ km}^2$ in size along the boundary were lumped in with a neighbouring cell resulting in a mean cell size of 63.9 km². During each trapping session, we placed 1 capture site in each cell for 14.1 (SE = 0.06) days on average. We conducted 4 consecutive trapping sessions within each cell between 30 May and 2 August 2000 in all but 1 of the 148 cells (1 cell was not sampled the first session because it was completely covered in snow) resulting in the sampling of 591 sites (Table 1, Fig. 1). Trap sites were moved within each cell for each session and we tried to ensure that each new site in a cell was located >1 km from all previous sites. We selected sites based on our subjective interpretation of the best grizzly bear habitat in that cell and the knowledge that grizzlies move up in elevation as summer progresses (Waller and Mace 1997, McLellan and Hovey 2001). We began fieldwork after all radiocollared grizzly bears were out of their dens and actively feeding (Ciarniello et al. 2001).

During the fall, we conducted additional sampling at 10 sites along 3 salmon spawning streams (Fontoniko, Herrick and James creeks) in the southern (Pacific) watershed of the mountains. Here, sites were checked every 4–5 days for 4 sessions (2 of the James Creek sites were not trapped in the first session), and were not moved between sessions. These sites were designed to sample bears at salmon spawning streams in order to examine capture efficiency and movements, and to investigate the feasibility of using fall sampling to provide an estimate of bears using these areas.

Field methods

We used Bell 206B helicopters, trucks, and all-terrain vehicles for access to sites. In helicopters we used a global positioning system (GPS)-geographic information system (GIS) computer navigation and mapping program (Poole et al. 1999) to facilitate navigation and site placement. We recorded the locations of all sites both manually on data forms and digitally with the computer program. Most locations were generated by hand-held GPS units and every effort was made to acquire 3-dimensional locations. We also used the GPS unit in the helicopter to map site locations. We placed sites near natural travel corridors whenever possible (alpine passes, valley bottoms, games trails, etc.). Site selection in the mountains covered the range from river valley bottoms to high passes between drainages, with a strong focus on avalanche chutes, especially during the first 2 sessions. In the plateau, site selection was restricted to road, seismic line, or pipeline access or suitable helicopter landing locations. We posted 2–4 warning signs at all sites where there was a risk of human encounter.

Hair collection sites consisted of liquid bait poured on a 1-1.5 m high mound of logs, stumps, moss and boughs (Poole et al. 2001). We surrounded the mound with a single strand of barbed wire running around 3 or more trees at about 50 cm from the ground (Woods et al. 1999). For bait we used about 250 ml of rancid fish oil and 3 to 4 litres of rotted cow blood. For the last 3 trapping sessions we added a novel scent to each site to encourage previously detected bears to revisit sites. In session 2 we used fennel oil, in session 3 we added skunk essence, and during the 4th session we placed 30 to 40 g of

Session	No. cells sampled	Start date	Mean sampling duration in days (SE)	No. of sites with grizzly bear hair (%)	No. of sites with black bear hair (%)	No. of sites where grizzly bear ID failed	No. of sites where black bear ID failed ¹
1	147	30 May	13.8 (0.09)	45 (31)	103 (70)	2	11
2	148	12 June	14.6 (0.11)	48 (32)	93 (63)	2	4
3	148	26 June	13.4 (0.13)	46 (31)	60 (41)	2	7
4	148	10 July	14.6 (0.10)	60 (41)	59 (40)	5	3
Grand mean			14.1 (0.06)	49.8 (34)	79 (53)		
Total	591			199	314	11	25

 Table 1. Bear hair capture results from the Parsnip/Herrick area, 2000.

¹ Only 205 of the 314 sites which detected black bears were run for genotypes due to budget constraints.

beaver (*Castor canadensis*) castor and essence of rotten egg at the site. We selected these scents based on trials using captive grizzly bears (Johnson and Kendell, in press). Scents were placed 2 m up in a tree within the site. Field crews carried pre-cut lengths of barbed wire; capture sites could be installed or removed in \leq 20 minutes by a 2-person crew.

During fall, hair sampling sites were placed along bear travel routes adjacent to Herrick (4 sites), Fontinko (2 sites), and James (4 sites) creeks, which were known to support runs of Chinook salmon. No bait was used, and 1–3 strands of wire were strung across sand bars or trails to remove hair from passing bears. Sites were set and checked during salmon enumeration flights between 16 August and 4 September 2000.

Before sites were removed, all hair from each barb was collected and placed in a small paper envelope. Samples that were within 2 barbs of each other were considered as part of the same group (an entry or exit point for a bear). We also collected hair from the ground below the wire and from sticks in the bait pile, especially when samples on the wire were few. Each sample was labelled as to group number and the location of the sample with respect to others in the group. All samples were air dried and either stored at room temperature until the end of the fieldwork, when they were placed in a freezer, or placed in a freezer immediately.

DNA analysis

Using a dissecting microscope, all hair samples were sorted into 3 categories: black bear, grizzly bear, and unknown bear species. Samples that contained no roots, or which were obviously not bear, were removed. We identified black bear samples by the presence of glossy black guard hairs with a solid black tip, and grizzly bears by brown guard hairs with grey or silver tips (Woods et al. 1999, Poole et al. 2001). Unknown samples contained hair that could not be unambiguously assigned to 1 species, or had no guard hair at all. Black bear samples were excluded from the first round of genetic analysis except for 50 samples that were retained to test the accuracy of visually sorting hair by species. Black bear samples were genotyped during a second round of analysis subsequent to grizzly bear genotyping.

We attempted to increase genotyping success and decrease typing errors by using at least 10 guard hairs in a sample (Boulanger 1998b, Boulanger and Himmer 2000, Mowat et al. 2000). If <5 guard hairs were available, then we added up to 30 underfur to the sample. Roots were clipped from guard hairs, but entire underfur were used for extraction. Occasionally, adjacent samples were combined if both samples had few hairs and these were the only samples available in that group. We did not extract adjacent samples, or samples separated by a single barb, because they are usually from the same bear (Boulanger and Himmer 2000). We tried to analyse every 3rd sample in a group of consecutive samples, but this varied depending on sample quality. We analysed at least 1 sample from each group of samples at a site unless there were more than 8 groups, in which case we usually chose the best samples from about 8 groups.

DNA analysis was conducted by Wildlife Genetics International (Edmonton, Alberta, Canada). DNA was extracted using DNeasy[™] Tissue kits (Qiagen Inc., Mississauga, Ontario, Canada). Species was confirmed using a length polymorphism in the mitochondrial DNA (mtDNA) control region (Paetkau and Strobeck 1996), or based on the results of the microsatellite marker G10J, whose allele sizes are diagnostic in separating among black and grizzly bears. In order to identify individual bears, each grizzly bear sample was analysed at 6 microsatellite markers (G1A, G10B, G1D, G10J, G10L and G10M) using methods described by Paetkau et al (1998). Another 6 markers (G10C, G10H, G10P, G10X, MU50 and MU59; Paetkau et al 1998, Taberlet et al. 1997) were screened on a small number of samples, and rejected due to lower variability or less robust amplification. For black bears we screened 12 microsatellite markers (G10C, G10H, G10J, G10L, G10X, G1A, G10B, G1D, G10M, G10P, MU50 and MU59) and used the 5 former markers for individual identity for the reasons given above. We used the sibling match test described by Woods et al. (1999) to measure the conditional probability that a full sibling of a given individual would have the same genotype. This conservative test was used because we knew that young bears often travel in sibling groups with their mothers. A new individual was recognised when a unique genotype had a *P* value <0.05 for the sibling match test. We declared 2 samples to be from the same bear when the genotype they had in common (i.e., excluding the loci that were incomplete for either animal) had a *P* value for the sibling match test <0.05. Samples were also excluded when they were missing data for more than 2 markers. This was done because such samples are prone to amplification errors (Taberlet et al. 1996; D. Paetkau, unpublished data) and normally fail to satisfy the aforementioned criterion for identifying samples from the same individual. In practice, the missing data rule obviated the probabilistic match criterion because *P* values were <0.05 for 4-locus genotypes in all but 1 case.

Genotyping errors were minimised by following the precautions outlined in Woods et al. (1999) and Poole et al. (2001). Sufficient data to allow individual identification were obtained for 860 grizzly bear samples of 1095 samples for which analysis was attempted (79% genotyping success). Of these 860 samples, 798 had genotypes that were not unique (i.e. matched the genotype obtained for 1 or more other samples). Since genotyping errors are unlikely to be reproduced, we presume that these 798 samples did not contain errors. However, 1 or more samples from each individual were reanalysed whenever a pair of individual genotypes matched at all but 1 locus. In addition, any of the 62 samples with unique genotypes were reanalysed if their genotype matched another genotype at all but 2 loci. This process uncovered a total of 19 errors. There were no cases where the same error occurred twice, and no cases where 2 errors were found in a single sample. On this basis we concluded that the probability of having 3 errors in a single sample was insignificant, and that our error-checking procedure should have identified all genotyping errors. We ran 691 samples for black bear identification and 571 (83%) generated acceptable genotypes after using the above error-checking procedure.

Once the process of identifying individuals was complete, 1 sample from each individual was selected for gender determination. Gender was identified using a length polymorphism in the Amelogenin gene that differentiates the X and Y chromosomes (Ennis and Gallagher 1994). Primers were modified to discourage the amplification of human DNA (D. Paetkau, unpublished data).

Statistical analysis

We used the mark-recapture models in program CAPTURE to test for capture variation and estimate population size. Because most collared grizzly bears had been darted from the air rather than snared, their capture was unlikely to have caused those individuals to avoid baited hair traps. A behavioural response was unlikely for hair captured bears because there was no food reward at a site and traps were moved each session. Therefore, we did not consider behaviour models during model selection. Time variation is easily detected in the absence of behavioural response. Heterogeneity of capture probabilities among individuals is more difficult to detect and can cause significant bias. We examined the tests in CAPTURE carefully for evidence of heterogeneity, while considering that these tests have low power when sample sizes are small (Otis et al. 1978, Boulanger and Krebs 1996). Prudence might suggest the use of a heterogeneity model in all cases (as suggested by Boulanger and McLellan 2001) because others have documented variation in capture probabilities among age classes of bear (Mace and Waller 1997), but heterogeneity models often show greater bias (Kendall 1999), especially when sample sizes are small, and often overestimates population size when no capture variation is present (Otis et al. 1978). Data were often too sparse to test for capture variation, nor were there adequate data to utilize a heterogeneity model with confidence (Manning et al. 1995). In these cases, the only models available for this dataset were time varying models, which would generate conservative results if heterogeneity was indeed present (Otis et al. 1978, Manning et al. 1995).

The program MARK was also used for estimation of population size when simple time models were used (White and Burnham 1999). The logit link was used for estimation. We estimated population size within the plateau and mountainous biophysical landscapes in the study area. Each unit formed a continuous portion of the greater study area, and we used the captures within each unit to estimate specific densities. We used logistic regression to test the relationship between the number of hairs in a sample and the probability of scoring a genotype. We used the logit function and tested assumptions regarding residuals. All analysis was conducted using SAS Version 6.12 (SAS Institute Inc., Cary, North Carolina, USA). Spatial analysis was conducted using ArcView and ArcInfo (Environmental Systems Research Institute, Redlands, California, USA).

We used Chao's Time and heterogeneity model when sample sizes were small because these models are designed for that purpose and, the Jackknife heterogeneity model is negatively biased with low sample size (Otus et al. 1978). We used Darroch's time model, as incorporated in CAPTURE and MARK when sample sizes were large because it generated lower variance. When both time and heterogeneity were indicated we used Chao's time and heterogeneity model. In some cases, when sample sizes were adequate, we ran estimates using both a time model and a time and heterogeneity model to demonstrate the outcomes of the 2 estimators.

Closure bias

Population estimates are biased upwards when the assumption of geographic closure is not met (White et al. 1982). We compared 3 different ways to correct for closure bias. The boundary strip correction was based on the idea that the area trapped is larger than the outer perimeter of the grid. In this case we increased the size of the grid to attempt to enclose the entire 'trapped area' or superpopulation (Dice 1938, Kendall 1999). Another way to approach the problem is to weight each animal captured by a measure of its residency on the study area as determined by radiotelemetry; this method has been developed by several authors (Eberhardt 1990, Garshelis 1992). We calculated residency for each individual as the proportion of radio locations which were on the study area; the corrected density was calculated by multiplying the naïve density by the mean residency for all radiocollared individuals (Kenward et al. 1981). Finally, we used the method presented by Boulanger and McLellan (2001) to correct for closure based on the average distance each individual was detected from the edge of the grid. This method has similarities to the nested grid approach presented by Otis et al. (1978).

Radiotelemetry data for the study area was used to calculate the average home range size (minimum convex polygon) of plateau males, plateau females, mountain males, and mountain females during the June and July hair collection. We used data for bears monitored in 1998, 1999 and 2000 because ranges changed little among years (Ciarniello et al. 2001). Home ranges were based on 6 to 19 telemetry locations/bear during June and July each year. Average home range size km² was 191 km² for plateau females (n = 9). 352 km² for plateau males (n = 7). 27 km² for mountain females (n = 38), and 166 km^2 for mountain males (n = 9). We calculated the radius of a circle equal to these average home range sizes for each sex, which we then used to extend the effective census area beyond the perimeter of the DNA sampling grid when calculating their respective densities (Dice 1938; see White et al. 1982 for a discussion of various similar methods). We did not buffer the sampling grid at the boundary between the plateau and mountain portions of the grid because both our radiotelemetry and DNA data indicated almost no movement of bears across this boundary during the June–July period. On average, this approach extended the effective census area to include the entire home range of any bears that spent half or more of their time in the grid. This buffering procedure increased the effective census area by 1.4 times for plateau females, 1.6 times for plateau males, 1.2 times for mountain females, and 1.4 times for mountain males.

We attempted to test the relationship between distance from edge and study area fidelity and immigration based on the methods of Boulanger and McLellan (2001). However, the methods were

complicated and notwithstanding several days of effort we were unable to reproduce these calculations. In the end, we simply calculated core population correction estimates by excluding a subset of bears based on their distance from the edge of the study area using 1 km interval increments. We then looked for a decline and levelling off in density with distance from edge, and choose the distance from edge based on where density began to level off. We did these calculations for the Parsnip-Herrick study, as well as for grizzly bears in the mountain (Northern Boreal Mountains ecoprovince of the northern Rocky Mountains) and boreal plains (Taiga Plains ecoprovince) portions of the Prophet River study area in northeastern British Columbia (Poole et al. 2001). Boulanger and McLellan (2001: Fig 4) present the same calculations for the Prophet River data, except that we did separate estimates for each sex and biophysical region because we felt each sex cohort was likely to demonstrate different closure bias, and we wanted density estimates for the mountains and boreal plains for comparative purposes. Further, Boulanger and McLellan (2001) suggest that their correction method assumes homogenous distribution of bears across the study area. The large difference in density between the 2 ecoregions makes homogeneity of distribution unlikely.

There was no indication of heterogeneity of capture probabilities in the complete Prophet River grizzly bear dataset (Poole et al. 2001), nor in the data for the mountainous portion of that study area, but sample size was too small to test for capture variation in the boreal plains. Boulanger and McLellan (2001) presented results that suggested there was heterogeneity in the combined dataset, but given that variation among sexes was small, we may have accounted for this variation by analyzing the 2 ecoprovinces separately. Regardless, except for the mountains with the sexes combined, sample sizes were too small to use a heterogeneity model. We present estimates for each sex and estimates with sexes combined because sample sizes were low (n = 15-68 captures) and capture probabilities were similar among sexes.

Population size using habitat based extrapolation

The Fuhr-Demarchi method is used by provincial management biologists to generate estimates of grizzly bear population size in order to set harvest quotas. This method involved assigning 1 of 5 density classes to each unique biogeoclimatic/ecosection combination in an area. This assigned density class represented the maximum potential grizzly bear carrying capacity, the habitat capability (Fuhr and Demarchi 1990). The 5 classes were 1–5, 6–25, 26–50, 51–75 and 76–100 bears/1,000 km². Habitat capability assignment was based on the biophysical characteristics of the area relative to the characteristics of the Flathead River area in southeastern British Columbia, where there were direct field-derived bear density estimates (McLellan 1994), and was standardized for the province by the Provincial Large Carnivore Research Biologist (T. Hamilton personal communication). Ministry of Water, Land, and Air Protection grizzly bear harvest management procedures required the use of the low end of the habitat capability class rating, but we also calculated Fuhr-Demarchi based estimates on the midpoint and maximum of the density class range.

Current carrying capacity was derived by stepping down the habitat capability ratings to account for the negative impacts of habitat loss, habitat alteration, and habitat displacement; the estimate of the number of bears was then determined by reducing the current carrying capacity to account for human caused mortality over the past 20 years (Ministry of Environment, Lands and Parks 1999). Accounting for the habitat loss, alteration, and displacement impacts followed the procedure specified by Matt Austin (no date), who was the Ministry of Water, Land, and Air Protection's Large Carnivore Specialist. For each of those factors a subjective estimate was made of the proportion of the area affected, the impact on carrying capacity (a number between 0.0 for no impact and 1.0 for complete loss to bears) and the value of the impacted area relative to the rest of the area being considered (1 if the area was average, 2 if it was twice as valuable as average, etc.). Lost habitat included the area covered by roads, urban development, agricultural crops, and recreational facilities, and by definition had an impact of 1.0. Habitat was

considered altered by forestry activities that reduced the availability of plant or animal foods, denning sites or resting sites. Displacement was defined as areas adjacent to lost habitat. The quantitative impact of these factors was determined sequentially by subtracting (stepping down) the proportional impacts from the habitat capability. Proportional impacts were calculated as the product of the area affected and the relative habitat value compared to carrying capacity.

We accounted for the impact of human caused mortality over the last 20 years by relating the number of bears shot, by resident and non-resident hunters and for wildlife control, to the maximum sustained yield specified in the provincial grizzly bear harvest management procedures (Ministry of Environment, Lands and Parks 1999). The number of bears shot by hunters and for wildlife control was known precisely because kill reporting was compulsory. The maximum sustained yield specified in the harvest management procedures was density-dependent and set at 3, 4, 5 or 6% per year for populations at 1–5, 6–25, 26–50 and >50 bears/1,000 km², respectively. Because many illegal kills are not reported (McLellan et al. 1999), we assumed that unreported kills accounted for 2% of the yield. We also assumed that the maximum sustained yield occurred at 80% of current carrying capacity (Taylor 1994). When the annual kill was greater than the sustainable yield, we reduced the population size accordingly, and if the kill was less than the sustainable annual yield then the population was reduced to between 80 and 100% of the current carrying capacity. The amount of the reduction was based on the ratio of actual kill to the maximum sustainable yield (i.e., if the actual kill was 0.5 of the yield then the final population estimate would be at 90% of the current carrying capacity).

We used the Fuhr-Demarchi method to estimate grizzly bear numbers for the plateau and mountains of the Parsnip-Herrick study area, and for the boreal plains and mountains of the Prophet River study area (Poole et al. 2001), and compared these estimates to DNA-based population estimates for each area.

RESULTS

Hair collection and analysis

We collected 5,955 hair samples from 439 sites within the Parsnip-Herrick study area. We ran mtDNA species tests on 1,450 samples which had been visually classified as grizzly bear or unknown bear. All 50 samples classified as black bear by visual characteristics were identified as black bears using the mtDNA species test. The technician working on the Parsnip samples was correct at visually classifying grizzly bear samples 81% (n = 565) of the time while a technician working on the Herrick samples was correct 87% (n = 513) of the time (Table 2). Six of the 671 samples (1%) we attempted to genotype for black bears turned out to be grizzly bears. We were more accurate at visually identifying black bear hair than we were for grizzly bear hair.

We identified grizzly bear hair at 199 sites; the proportion of sites that removed at least 1 grizzly bear hair sample was highest during the last session (Table 1). Within the mountains, 177 out of 403 sites collected a grizzly bear hair sample (44%), and on the plateau 22/188 sites (12%) collected grizzly bear hair. We identified black bear hair at 314 sites, with proportionately more detections in the plateau (76%; n = 188 sites) than the mountains (43%, n = 403 sites; Fig. 2). In the mountains, the number of sites that detected black bears each session decreased as the study progressed, because we moved our sites to higher elevations each session.

DNA fingerprinting resulted in the identification of 239 grizzly bears and 275 black bears. There were 11 sites that removed grizzly bear hair but where we were unable to identify an individual (Table 1). An average of 1.9 grizzlies was detected at each site that captured grizzly bear hair, with no apparent trend throughout the study (range 1.7–2.2 bears/successful site). Eighty-six grizzly bears were detected at >1 site and up to 8 grizzlies were detected at a single site (2 sites). Thirty-five black bears were detected at multiple sites and up to 5 black bears were detected a single site. The overall grizzly bear sex ratio for

the plateau and the mountains combined was 35M:65F (n = 237), which was almost identical to the sex ratio of live-captured grizzly bears (33M:67F, n = 42; Ciarniello et al. 2001). The sex ratio of DNA-identified black bears was (45M:55F, n = 194) on the plateau and (41M:59F, n = 85) in the mountains.

The number of scoreable alleles per sample was positively related to both the number of guard hairs and underfur in a sample (n = 738, r = 0.21, P = 0.0001, and n = 384, r = 0.17, P = 0.001, respectively). After excluding samples that contained both guard and underfur, we found that genotyping success was positively related to the number of hairs that went into a sample, for both guard hair and underfur (Figs. 3, 4). The logistic regression model was significant for both guard hair and underfur roots (n = 678, $\chi^2 = 17.6$, 1 df, P = 0.0001, and n = 372, $\chi^2 = 15.9$, 1 df, P = 0.0001, respectively).

Area		Species identification based on mtDNA (%)					
Sorting ID^1 n		Black bear	Grizzly bear	Other ²			
Parsnip							
Black bear	50	50 (100)	0	0			
Grizzly bear	563	106 (18.8)	456 (81.0)	1 (0.2)			
Both bear species	18	10 (55.6)	8 (44.4)				
Unknown bear	44	28 (63.6)	13 (29.6)	3 (6.8)			
Herrick							
Black bear	0^3						
Grizzly bear	513	66 (12.9)	446 (86.9)	1 (0.2)			
Unknown bear	124	34 (27.4)	86 (69.4)	4 (3.2)			

 Table 2. Comparison of species identification of bear hair using macroscopic sort and DNA species testing, Parsnip/Herrick grizzly bear DNA inventory, 2000.

¹ Hair samples were visually sorted into black bear, grizzly bear and unknown based on gross hair morphology and colour.

² Other samples were species other than bear.

³ No samples identified as black bear during macroscopic sorting of the Herrick samples were tested using mtDNA.



Figure 2. Parsnip/Herrick bear DNA inventory study area and site locations, 2000. Sites that detected black bears are shown in solid circles, with proportionately larger circles depicting sites with the number of individuals detected (1–5 bears). Sites that did not detect black bears are shown in open circles. The irregular line along the Parsnip River shows the approximate boundary between the plateau and mountains. The height of land between the Pacific and Arctic drainages of the Hart Ranges is shown running west of Monkman Provincial Park; black bears were not genotyped south of this line and solid circles indicate black bear presence here.



Figure 3. The relationship between the number of guard hair roots put into a DNA sample and the probability of generating a 6 loci genotype (mean <u>+</u>95% CI) as calculated using logistic regression.



Figure 4. The relationship between the number of underfur roots put into a DNA sample and the probability of generating a 6 loci genotype (mean $\pm 95\%$ CI) as calculated using logistic regression.

Population estimation for grizzly bears

We captured 21 grizzly bears (13 M, 8 F) 24 times on the plateau (Fig. 5a). None of the 4 radiocollared grizzly bears known to be in the study area, based on retrospective examination of their locations, were captured during hair sampling. Three radiocollared bears spent >50% of their time on the plateau portion during our study, hence the total number of grizzly bears known to be on the plateau during our study was 24.

We could not use radiotelemetry data to calculate residency or correct for closure on the plateau because only 4 radiocollared grizzlies were resident during this study, which, notwithstanding the small sample size, are not likely a representative sample because trapping effort and live capture success were not even across the area. Consequently, only 57% of the radiolocations of these 4 bears were on the study area during our study period. Core correction for the plateau did not demonstrate any evidence of closure bias (Fig. 6a); closure bias may have been small, or the small sample size may have rendered the bias undetectable. Total captures were only 14 for the smallest core area, 7 km from the boundary. We felt this closure correction technique was unreliable for the plateau grizzly bears. Our only option to correct for closure bias for grizzly bears on the plateau, we assumed that the naïve estimated 50 bears had the same 35:65 male:female ratio that we recorded over the entire grid area. The corrected population density for the plateau was 12 bears/1,000 km² (95% confidence interval [CI] 7–28; Table 3). Average capture probability was 0.12.

Sample sizes were much larger in the mountainous portion of the study area (Fig. 5b). Both datasets had reasonably large samples sizes (n = 106 and 193 captures, respectively) and modest capture probabilities ($\overline{\chi} = 0.22$ and 0.21, respectively), so we expected reasonable power to detect capture variation. Neither of the closure tests in CAPTURE detected closure violation for either sex in the mountains (P > 0.16). Initial population estimates suggested that grizzly bear densities did not differ (<5%) between the Hart Ranges within the Parsnip and Herrick areas, thus we estimated density for the entire mountainous region. Within the mountains we calculated separate estimates for males (n = 76 individuals) and females (n = 140) in order to reduce capture variation and allow for more realistic correction for closure bias. We identified 216 different grizzly bears in the mountain portion of our study during hair sampling. Eight of 12 radiocollared grizzlies were detected in hair sampling giving an overall detection probability of 0.67, which is similar to the overall detection probability of hair sampled bears (0.63). Two grizzly bears were shot in the Herrick portion of the study area during the first 13 days of June.

We compared 3 different methods to correct for closure bias in the mountains. The boundary strip correction method resulted in reductions of 15 and 29% for female and male grizzly bears in the mountains, respectively, compared to the naïve density estimates (Table 3). We used radiotelemetry data to assess closure along a single border of the mountainous portion of our study area because collared bears all resided on the northeast boundary of our study area and cannot be considered a representative sample from our entire population of bears. There were sufficient locations ($\bar{x} = 11$ locations, range 6–13) to determine study area residency for 12 grizzly bears resident in the mountains; only 1 of these bears was male. These 12 bears spent 93.1% of their time on the study area. We reduced both the male and female population estimate for this study area by 7% for the portion of the study area boundary that was not closed (64%). We assumed complete closure along the west boundary because only 1 movement across this boundary was detected in our data, and density on the plateau was low. We also assumed that a small portion (4%) of the southern border was closed because it was glaciated. Using the radiotelemetry correction method we obtained a density of 51 bears/1,000 km², a reduction of 5 and 4% for female and male grizzly bears, respectively (Table 3).



Figure 5. Total captures and % new captures for: a) Fraser Basin grizzly bears, b) Hart Ranges grizzly bears, c) Fraser Basin black bears, d) Hart Ranges black bears. Only 1 black bear was identified in the 4th session in the Hart Ranges, hence the 3rd and 4th sessions were combined.



Figure 6. Core population corrected population estimates for: a) Fraser Basin grizzly bears, b) Hart Ranges grizzly bears, c) Fraser Basin black bears, d) Hart Ranges black bears, e) Taiga Plains grizzly bears, f) Northern Boreal Mountains grizzly bears. The first 4 figures are calculated from data collected in the Parsnip and Herrick Rivers summer 2000. The last 2 figures are reanalyses of data from the Prophet River area of northeastern British Columbia (Poole et al. 2001). Each estimate is calculated by removing bears whose mean capture distance (in km) is within the given distance from the edge of the study area boundary and then extrapolating the estimate of the reduced area to the full study area (Boulanger and McLellen 2001).

Table 3. Correcting population density of grizzly bears to account for closure bias using boundary strips (Dice 1938), radiotelemetry movement data (Kenward et al. 1983), and the core population methods (Boulanger and McLellan 2001). Inhospitable habitat (rock, ice, and lakes) was subtracted from study area size to calculate all densities.

	Plateau females	Plateau males	Plateau males and females	Mountain females	Mountain males	Mountain males and females
Naïve Density (bears/1,000 km ² ; 95% CI)	11.1 ^a	6.0 ^b	17.1 (9.6– 40.4)	35.0 (30.1– 42.7)	19.0 (15.7– 25.0)	53.9 (45.8– 67.7)
Boundary Strip Correction						
Hospitable area within grid (km ²)	2932	2932	2932	6322	6322	6322
Average radius of home range (km)	7.8	10.6		2.9	7.2	
Hospitable area of buffer adjacent to grid (km ²)	1257	1752		1100	2637	
Corrected density	7.8 ^a	3.7 ^b	11.5 (6.7– 28)	29.8 (25.6– 36.4) ^c	13.4 (11.1– 17.6) ^c	43.2 (36.7– 54.0) ^d
Radiotelemetry Correction						
Corrected density	na	na	na	33.4 (28.6– 40.8)	18.2 (15.0– 23.9)	50.6 (43.6– 64.7)
Core Population Correction						
Corrected density	na	na	na	32.4 (28.5– 37.3)	16.8 (14.4– 21.5)	49.2 (42.9– 58.8)

^a Assuming females comprise 65% of population.

^b Assuming males comprise 35% of population.

^c Based on individual mark-recapture estimates for each sex cohort.

^d Derived by adding the point estimates and CIs for each sex.

Mountain grizzly bear population size declined measurably using a 1 km interior boundary to correct for closure bias for females and a 2 km boundary for males, and then changed little using smaller core populations (Fig. 6b). We used the 1 km core population estimate to calculate density for females and the 2 km estimate to calculate density for males, resulting in a density of 49 bears/1,000 km² (CI 43–59), a reduction of 7 and 12% from the naïve density estimates for female and male grizzly bears, respectively (Table 3). Use of model M_{th} would have generated similar corrected estimates even though M_{th} generated larger estimates for females for many core populations (Fig. 6b). We believe the core corrected density is most accurate of the 3 closure correction methods because the buffer strip method is likely conservative and the radiotelemetry sample was biased towards females and was too small and clumped to provide an accurate correction.

Population estimation for black bears

We captured 194 black bears 216 times on the plateau; capture probabilities were higher for males than females and captures were fewer in the last 2 trapping sessions for both sexes (Fig. 5c). We did separate population estimates for the sexes to reduce capture variation and infer closure bias by sex.

Core population estimates suggest that closure greatly biased the population estimate for both males and female black bears (Fig. 6c). For males, Chao's M_{th} model is likely more accurate than the simple time model because heterogeneity was mildly suggested. Both the time model and M_{th} generate the same estimates for females. Changes in population estimates using increasing boundary strips suggest the use of the 3 km core estimate for female black bears and the 5 km estimate for males (Fig. 6c). However, this means closure bias of 22% for females and 55% for males, which is highly unlikely given the large study area and relatively small home ranges of black bears in wet ecosystems (Pelton 1983, Kolenosky and Strathern 1987). Given the small number of recaptures in this dataset, stochastic events may have lead to declines in the estimate with distance from edge. Therefore, we used the 1 km buffer, combined sexes, and Chao's M_{th} to estimate population size for the plateau as 793 black bears (CI 506–1,344), which yields a density of 270 bears/1,000 km² (CI 173–458).

Eighty-five black bears were captured 90 times during the 4 capture sessions in the mountains. Capture success declined each session; only 1 black bear was captured during the last session (Fig. 5d). We combined sessions 3 and 4 and used Chao's time model to estimate population size because capture success was low in the last session and time variation was obvious. Core corrected estimates generate a sharp initial decline in population size by excluding bears within 1 km of the border, and the estimates were roughly equal for the next 4 core calculations (Fig. 6d). Using the 1 km core corrected estimate suggests a closure bias of 28% and, here again the low numbers of recaptures makes such an estimate suspect. We elected not to correct for closure because recaptures were few; black bear density was 100 bears/1,000 km² (CI 55-210) in the mountains.

Closure correction for Prophet River grizzly bears

For the boreal plains portion of the Prophet River study area, there was a small decline in estimated core corrected population size of grizzly bears up to 2 km inside the study area, but the population estimates increased using data from 3–9 km inside the boundary (Fig. 6e). We used the 2 km corrected estimate to estimate population size for the boreal plains because this is where the initial decline stopped. Population size was estimated at 53 (CI 39-89) and density was 10 bears/1,000 km² (CI 7–16); virtually identical to the density presented by Poole et al. (2001).

Using the core population correction for the mountainous portion of the Prophet River study area, there is a sizable decline in population size up 6 km inside the study area and numbers increase from 6–9 km inside the boundary (Fig. 6f). We used the 6 km corrected estimate to estimate grizzly bear population size for the Prophet Mountains because this is where the initial decline stopped. We used the time varying model with the 2 sexes combined because sample sizes were very low for individual sexes with data 6 km in from the boundary. The heterogeneity model generated virtually identical estimates (Fig. 6f). The final estimate was 70 grizzly bears (CI 63–91), which generates a density of 22.5 bears/1,000 km² (CI 20–29), 22% lower than the density presented by Poole et al. (2001).

Fuhr-Demarchi population estimates

Habitat capability ratings for the 15 biogeoclimatic/ecosection zones in the plateau and mountains of the Parsnip-Herrick study area ranged from 1 to 5, resulting in a maximum potential population size of 279–429 bears in the mountains and 59–126 bears on the plateau (Fig. 7a). The Fuhr-Demarchi population estimation method indicated that the impact of habitat loss, alteration and displacement reduced the carrying capacity to 255–393 in the mountains and 35–77 on the plateau; habitat loss was primarily related to road abundance. There were no roads in the alpine and few in the ESSF, with about 5% of the SBS being roaded except in the SBSmk1NEL where the town of Bear Lake and its associated industrial sites covered about 7% of the area. By definition, loss impact in these roaded areas was 1.0 and, in general, roads were in areas we considered as representative bear habitat, so we assigned a relative habitat value of 1.0. However, in the ESSFwk2HAR, roads were primarily in valleys that we judged to be only half as good for bears as average, so we assigned a relative habitat value of 0.5.

Logging may adversely alter bear habitat value by changing natural succession patterns and forest age class distributions. We judged that logging reduced the value of 2% of the ESSFwk2HAR but, again, because logging occurred primarily in valleys that we judge to be only half as good as average for bears, we assigned a relative habitat impact value of 0.5. In most of the study area we judged that logging altered 30% of the area and that the altered area was representative bear habitat.

Some bears may be displaced from roads and other areas used by humans. The proportion of the area from which bears were displaced depended on road density with the road's zone of influence probably affecting 100% of the area where road density was highest. Where there was active logging and therefore high traffic volume, we estimated the impact at 50% (i.e., only half the bears were displaced or bears were displaced for only half of the time), and where there was less active logging and less traffic we estimated the impact at 10%. We did not consider fragmentation effects separately but we linked fragmentation impacts with habitat displacement impacts.

Incorporating known hunting kills, averaging 7 grizzly bears/year in the mountains and 2.5/year on the plateau, resulted in stepped down Fuhr-Demarchi population estimates to between 192 and 369 bears for the mountains and 0 and 50 bears on the plateau (Fig. 7a). These estimates convert to 30-57 grizzly bears/1,000 km² and 0-17 bears/1,000 km² for the mountains and plateau, respectively.

Using a similar rationale, we calculated a stepped down Fuhr-Demarchi population estimate for the mountains and boreal plains of the Prophet River study area, and obtained estimated grizzly bear populations of 0 to 130 bears for the boreal plains and 0 bears for the mountains (low to high end of the capability rating range; Figs. 7b and 7c). These estimates translate into 0-22 grizzly bears/1,000 km² and 0 bears/1,000 km² for the boreal plains and mountains, respectively. The harvest step-down usually caused the greatest reduction in the population estimate and therefore the largest reason for the disagreement between the DNA-based and habitat-based population estimates (Fig. 7).

Bear movements

Eighty-six grizzly bears were detected more than once (up to 4 times) during the Parsnip-Herrick study. Within the mountains, the average movement by males was over twice that for females (Table 4). No recaptures of males occurred on the plateau. Six movements were detected between the mountainous portions of the Parsnip and Herrick study areas. Only 1 grizzly bear crossed the boundary between the mountain and plateau regions, a male that moved from well inside the mountains to well inside the plateau and back again during the study. Only 3 grizzly bears were captured at sites close (<2 km) to the boundary between the mountains and plateau regions. One long-distance movement was detected; a male bear that moved 111 km from the Sukunka River valley in the northeast corner of the study area to the McGregor River in the southern end of the study between sessions 1 and 3.





Figure 7. Grizzly bear population estimates based on the Fuhr-Demarchi habitat-based extrapolation method for mountainous and plateau/boreal plains habitats in the Parsnip-Herrick study area (A: upper series of lines for the mountains, lower for the plateau) and Prophet River study area (B: mountains, and C: boreal plains), British Columbia. Lines represent stepped down bear estimates, starting from the high, midpoint and low end of habitat capability ratings for each. Step 5 is the estimated habitat carrying capacity, Step 6 accounts for bear mortality. Horizontal lines at "Step 7" represent the DNA-derived point estimates (\pm SE).

Biophysical region ^a	Species	Sex	п	Mean	SE	Range
Hart Ranges	Grizzly	Male	45	13.1	2.38	1.6–110.7
	Grizzly	Female	75	5.3	0.57	0.8–38.1
Fraser Basin	Grizzly	Male	0			
	Grizzly	Female	3	4.6	1.92	1.1–7.7
Hart Ranges	Black	Male ^b	7	8.1	1.33	4.6-12.9
	Black	Female	5	4.3	0.40	3.1–5.4
Fraser Basin	Black	Male	16	4.6	0.50	2.2-8.3
	Black	Female	6	2.7	0.49	1.6–4.8

Table 4. Distance moved (km) between capture locations for grizzly and black bears by biophysical region and sex in the Parsnip/Herrick area in 2000.

^a In addition, 1 male grizzly bear was detected moving from the mountains to the plateau (34.0 km), and back to the mountains (28.6 km).

^b One male black bear that moved 40 km across the Hart Mountains to the edge of the Fraser Basin was excluded because we felt it was not a territorial movement.

Black bear movements in the Parsnip-Herrick study were shorter than grizzlies, and like grizzlies, females did not move as far as males (Table 4). One male black bear moved 40 km across the entire mountainous portion of the study area. Three black bears were detected moving across the mountain-plateau boundary, although all 3 movements were within 2.4 km of the boundary.

Fall sampling

During fall hair sampling, grizzly bear hair was collected at 7 of 10 sites (Fig. 8). Black bear hair was detected at only 1 site, which did not detect a grizzly bear. Eighty-nine hair samples were collected, from which 15 grizzly bears were identified (9 M, 6 F). Four bears were recaptured within the fall samplings, all on the same creeks as originally detected. At 4 sites we removed grizzly bear hair but we were unable to identify an individual. Hair samples from the fall were generally of lower quality than the summer samples, more hairs were required to score all 6 loci. Nine of the 15 bears identified were captured at sites along James Creek (Fig. 8).

We combined the third and fourth capture sessions to calculate grizzly bear population size along these creeks because only 1 bear was captured during the last session. We estimated that 21 grizzly bears (CI 16–44) used the 47 km of creek that we trapped in fall.

Eleven of the 15 fall-captured bears (6 M, 5 F) had been detected previously (Fig. 8). Distance between their last summer capture (in the event of multiple summer captures) and fall capture was greater for males ($\overline{\chi} = 18.6$ km; range 4.0–48.3 km) than for females ($\overline{\chi} = 4.8$ km; range 0.3–7.5 km). Two male grizzly bears made long-distance movements from the upper Missinka River (35 km) and upper Framstead Creek (48 km) to James Creek (Fig. 8).



Figure 8. Fall grizzly bear hair sampling sites in the Herrick Creek area, 2000. June and July hair sampling sites are shown with open and closed circles. Fall hair sampling sites that detected grizzly bears are shown in solid squares, with proportionately larger circles depicting sites with the number of individuals detected (1–7 bears). Sites that did not detect grizzly bears are shown in solid triangles. J = James Creek; F = Fontoniko Creek; H = Herrick Creek. Heavy lines show movements of grizzly bears captured during summer (June–July) trapping and subsequently during fall sampling, and their last summer capture location prior to the fall.

DISCUSSION

Population density

The grizzly bear density estimate we obtained for the Hart Ranges was similar to other areas along the west slopes of the Rocky Mountains (Table 5). Small study areas are often placed in higher quality habitats than surrounding areas (Smallwood and Schonewald 1996), hence some of the densities reported in the literature are likely higher than would be found in the surrounding landscape. Although much lower than the mountains, grizzly bear density on the plateau of the Fraser Basin was similar to densities in other boreal or sub-boreal plains in British Columbia and Alberta (Table 5). Others areas of the interior distribution of grizzly bears, such as the east slopes of the Rocky Mountain and discontinuous populations in the south of the species range, also support lower bears densities (Table 5; LeFranc et al. 1987). Densities of coastal bear populations are usually much higher than observed in the continental interior (MacHutchon et al. 1993, Miller et al. 1997), although Boulanger and Himmer (2001) report densities similar to the Rocky Mountain West Slopes for an area of southwest British Columbia. Densities in interior Alaska are highly variable; some areas have densities similar to the Rocky Mountain west slopes, while others are lower than documented in the sub-boreal plains (Miller et al. 1997).

Observed patterns in grizzly bear density may be explained by ecosystem productivity and human impact. Bear density is moderate to low in all the discontinuous populations that have been studied along the southern edge of the bears range (Table 5, LeFranc et al. 1987). Densities in these discontinuous populations are likely limited by the effects of fragmentation and ongoing human impacts, not necessarily lower habitat productivity. All 4 densities from discontinuous populations in Table 5 are from areas in the west slopes of the Rocky Mountains (Table 5), and have similar habitat quality to adjacent areas to the north. Proctor et al. (2002) showed that bears in the southern portion of the Central Selkirk Mountains are at least partially isolated from the adjacent population to the north. We reanalyzed data from Mowat and Strobeck (2000) to compare density among the more isolated south and less isolated north (Table 5); densities in the less isolated north are approximately double those in the south despite similar habitat. Habitat quality may be secondary to human impact in predicting bear density in the southern portion of the grizzly bear's distribution.

Further north along the interior mountains bear densities are consistently higher on the windward side of the continental divide than in the rain shadow on the leeward side to the east, likely a result of the reduced rainfall and hence reduced vegetative production in the rain shadow of the large interior mountains (Hamer and Herrero 1987, Hamer et al. 1991). The singe study area with estimated bear density >20 bears/1,000 km² on the east side of the continental divide is in the Prophet River area of the Northern Rocky Mountains (Table 5).

Grizzly densities are low in the boreal and sub-boreal plains in British Columbia and Alberta. Many of these areas have also been heavily impacted by humans, which may partially explain the consistently low densities. However, the boreal plains of the Prophet River were only mildly impacted by people (Poole et al. 2001) and here too, densities were low.

Many coastal areas have much higher densities than documented in the interior (MacHutcon et al. 1993, Miller et al. 1997) likely due to the longer growing season, greater rainfall, and abundant salmon runs. We showed that grizzly bears will move long distances to feed on salmon and that bears can be very abundant along interior salmon streams. We did not, however, find greater landscape scale density between the Pacific and Arctic drainages in the non-salmon season.

	Density (b	ears/1,000 km ²)		
			Study area	
	Mean	95%CI	size (km ²)	Reference
Rocky Mountain west slopes and				
adjacent ranges	16 00		120	M-L-11 1090
Flathead Valley, B.C.	46-80	20.02	130	McLellan 1989
Flathead Valley	48	30-92	3,233	Boulanger 2001a
Hart Ranges, B.C.	49	43-59	6,436	This study
Northern Central Selkirk	48	30–90	4,640	Recalculated from Mowat
Mountains, B.C.	26 55		1.	and Strobeck 2000
Glacier National Park, B.C.	36-33		unk	cited in LeFranc et al. (1987)
Central Columbia Mountains, B.C.	34		354	Simpson et al. 1985
Glacier National Park, Montana	32		1,044	Martinka 1974
Central Purcell Mountains, B.C.	25	22–40	1,650	Strom et al. 1999
Central Columbia Mountains, B.C.	19	13–39	4,096	Woods et al. 1999, Boulanger 2001b
Rocky Mountain east slopes				
Northern Canadian Rocky	23	20–29		Poole et al. (2001); this study
Mountains, B.C.				
Jasper-Cadomin, Alberta	19	12–35	5,352	Mowat et al. 2000
Kananaskis, Alberta	16		254	Wielgus and Bunnell 1994
Southwest Alberta	15	12-20	5,030	Mowat and Strobeck 2000
Kananaskis, Alberta	10			Eastern Slopes Grizzly Bear Project 1998
Jasper National Park, Alberta	10		1,625	Russell et al. 1979
Banff National Park, Alberta	10			Gibeau et al. 1996
Discontinuous populations in the				
Rocky Mountain west slopes				
South Selkirk Mountains, B.C.	23		235	Wielgus et al. 1994
Southern Central Selkirk	19	12–37	5,226	Recalculated from Mowat
Swan Mountains, Montana	16		1 / 157	Mace and Waller 1998
South Solkirk Mountains, WA ID	10		1,457	Wielgus et al. 1004
Borool and sub borool plains	14		100	Wieigus et al. 1994
Leaner Derk and sector footbills	10 ^a		5 250	More at al. (2000)
Alberta	19		3,332	Mowat et al. (2000)
Fraser Basin, B.C.	12	7–28	3,016	This study
Prophet River boreal plains, B.C.	10	7–16	5,518	Poole et al. (2001); this study
Swan Hills, Alberta	10		unk	Nagy and Gunson (1990)
South Wapiti River, Alberta	7		unk	Nagy and Gunson (1990)

Table 5. Reported bear densities in and near the Rocky Mountains of North America.

^a This is likely an overestimate of density on the boreal plateau because their study area included both boreal plateau and Rocky Mountain east slope habitat, and the east slopes appeared to have higher numbers of bears than the plateau.

The pattern of black bear densities is opposite to that of grizzly bears, with estimated black bear density about 3 times greater in the plateau of the Parsnip study than in the Hart Ranges. Even in the mountains, black bears were captured in valley bottoms (Fig. 2). The low number of captures in the mountains in the third and fourth trapping sessions was because we tended to move our sites higher in elevation through the study, and black bears were rarely detected near or above treeline. This may be due to competitive exclusion by grizzly bears, since we have observed black bears using alpine and sub-alpine areas outside the distribution of grizzly bears (G. Mowat, personal observation). Also, grizzly bears appeared to exclude black bears from near salmon streams when salmon were running; black bears were detected at 8 sites along these streams during June and July but only 1 black bear was detected along the salmon streams in the fall. Others have made similar observations along coastal salmon streams (Miller et al. 1997, Jacoby et al. 1999).

Little work has been done on black bear population characteristics in British Columbia. Miller et al. (1997) estimated black bear density to be 89 bears/1,000 km² (CI 77–103) in a relatively flat, partially forested area of interior Alaska. This is much lower than the black bear density we found in the plateau portion of our study area; however, black bears in their study area existed in creek bottoms and forested strips, similar to our mountain population. Also, grizzly bear density was considerably higher in the Alaska study area than in the plateau portion of our area. Miller et al. (1997) reported black bears densities similar to our plateau estimate in 2 areas of coastal Alaska. Kolenosky and Strathern (1987) report densities from 200–1,300 black bears/1,000 km² in the Pacific Northwest, with the highest density reported for coastal Washington. Our data supports the suggestion by Miller et al. (1997) that black bears occur at higher densities than grizzlies in the interior and that black bears are most abundant where grizzly bears are rare or absent.

A comparison of the DNA-based and Fuhr-Demarchi grizzly bear estimates for the Parsnip-Herrick and the Prophet River study areas shows that in all 4 cases the DNA-derived population estimates are higher than the Fuhr-Demarchi estimates used for bear management in British Columbia (using the low end of the capability range), but similar to Fuhr-Demarchi estimates using the medium habitat capability range (Fig. 9). Use of the low end of the initial habitat capability class rating, as is government policy, resulted in such a low estimate that the known hunting kills would have eliminated bears from all but the mountains of the Parsnip/Herrick study. Mean harvest over the last 10 years was <3% of the DNA-based estimate for the Hart Ranges, well below both the maximum sustainable yield of 5.7% (Miller 1990:357) and the maximum harvest allowed by the British Columbia government's harvest management procedures. However, harvests were 7 to 11% of the point estimate for the Prophet Mountains and both plateau areas, all well above what is considered sustainable. Use of the midpoints of the initial habitat capability class ratings results in Fuhr-Demarchi estimates between 0 and 93% of the DNA estimates. The low end of the capability rating, i.e., before any of the step-downs are applied, results in estimated bear densities in mountainous portions of both the Parsnip-Herrick and Prophet study areas that are lower than the DNA-derived estimates for those areas (Figs. 7a and 7b).

Because the DNA estimates presented here are so much higher than the Fuhr-Demarchi estimates, the British Columbia Wildlife Branch procedures appear to result in a conservative approach to bear management. But the subjective nature of the Fuhr-Demarchi method precludes the generalization that the application of this method will always underestimate bear population size; for example, Boulanger and Hamilton (unpublished data) generated different results than ours for the Prophet River study area. The subjectivity of the procedure and the limited number of density options available for capability rating suggest that Fuhr-Demarchi derived numbers will not necessarily be correlated in any way to direct field estimates. Our data cannot be used to objectively revise the Fuhr-Demarchi method to make it more accurate because there are so many subjective steps in the process. For example, we cannot differentiate from our data whether the plateau in the Parsnip-Herrick study has a lower capability to support grizzly bears than the mountains, if the low plateau densities are a result of human disturbance, hunting or current forest successional stage, or some combination of those and/or other factors.



Figure 9. Grizzly bear population estimates and numbers from the Fuhr-Demarchi extrapolation method from the Parsnip/Herrick and Prophet River areas (Poole et al. 2001) by biophysical region. The bottom figure shows the data with the Parsnip/Herrick Mountains (Hart Ranges) removed. The range of the DNA-based estimates is presented by the 95% confidence intervals (the point estimate is in the middle point). The range of Fuhr-Demarchi extrapolations are based on stepped down calculations from the low, mid- and high ends of habitat capability ratings. Heavy solid circles represent the point estimate from the DNA-based inventory and the low of the Fuhr-Demarchi method (the value prescribe for use in bear management by the British Columbia Wildlife Branch). Dotted line represents the 1:1 line of agreement between estimate methods.

Hunter selection for male bears in our study area may have contributed to the preponderance of females in the live population. But a similarly biased sex ratio in the kill in the Prophet River area (63:37, n = 272, British Columbia Ministry of Water, Lands and Air Protection unpublished data) did not appear to distort the sex ratio there (Poole et al 2001). Where sample sizes are large, most grizzly bear sex ratio estimates show a preponderance of females (McLellan 1989, Aune et al. 1985, 1986 cited in LeFranc et al. 1987;49, Woods et al. 1999, Mowat and Strobeck 2000, Mowat et al. 2000), although LeFranc et al. (1987; for Yellowstone), Woods et al. (1999) and Poole et al. (2001) all document more even sex ratios. Reduced survival of sub-adult males may also contribute to sex ratio bias (McLellan et al. 1999).

Movements

We detected only 1 grizzly bear moving between the mountains and plateau in the Parsnip study area, which is consistent with movements of radioed bears in this area (Ciarniello et al. 2001) and results in the Prophet River area (Poole et al. 2001). Movement between mountainous and plateau ecosystems in spring and early summer may be rare. Females did not move as far as males, which is expected given their smaller home ranges (Nagy and Haroldson 1989, Ciarniello et al. 2001), and is also consistent with results from the Northern Rocky Mountains (Poole et al. 2001). Black bear movements were smaller than that of grizzly bears, which suggests they have smaller home ranges.

The 2 furthest movements by grizzly bears detected from summer to fall (35 and 48 km) demonstrate that interior male grizzlies will move long distances to obtain fish when salmon are running. These movements were detected with only relatively few capture events (19) and on short stretches of river that harbour only modest salmon runs compared to other runs in the upper Fraser River basin (B. Toth, personal communication). Further, the number of bears that used the 47 km of stream we trapped was large, which suggests considerable concentration of bears during the salmon spawning season. Females did not appear to leave their home ranges to reach salmon, although it seems likely that the above 2 males made extra-territorial movements to fish for salmon. Hilderbrand et al. (1999) demonstrate that fall salmon availability is related to many life history traits of grizzly bears, including density.

Closure

The boundary strip method generated more conservative estimates of density than the radiotelemetry or core population corrections. We subjectively adjusted the boundary strip calculations based on our observation of essentially no bear movements along the plateau-mountains boundary and the presence of glaciers along portions of the boundary; the corrections would have been even more conservative had we not done this. Indiscriminate application of a boundary correction factor can greatly overestimate closure bias if portions of a boundary are indeed closed or uninhabited by the study species (Boutin 1984). Perhaps residency was heterogeneous along the boundary and our rather coarse application of a boundary strip overestimated the amount of permeable boundary. In contrast, the modest reduction in predicted population size using concentric increases in distance from edge suggests that lack of closure only biased population estimates within about 1 km from the study area boundary (Fig. 6b). Corrected estimates for buffers 2–7 km inside the study area were similar, so the choice of the buffer distance had little effect on the estimated density. Buffers larger than 7 km predicted lower population sizes, especially for females; however, these effects are more likely due to the reduction in sample size than closure bias.

Kendall (1999) shows that most closed model estimators can provide unbiased estimates of the "superpopulation" if movements on and off the study area are completely random. Kendall's superpopulation is essentially all individuals that are available for capture during the study, which presumably includes some portion of the residents along the boundary. Hence we still need to define the "trappable area" if we are to provide an unbiased estimate of density. The boundary strip method

attempts to define the trappable area. Kendall (1999) also argued that closure violation would add heterogeneity to capture probabilities, necessitating the use of models that accommodate this form of capture variation. We suspect individuals with very low capture probabilities (who presumably have only a small portion of their home range on the study area) are few when the grid is large relative to home range size, and that is why we did not detect heterogeneity in our data. However, when the mean capture probability is low, differences between the mean probability and those of edge bears may be small, making it difficult to detect the heterogeneity caused by edge bears. It seems likely that bears which have only a very small portion of their home range on the study area have capture probabilities so low that they are not accounted for in the mark-recapture model; which is the desirable result if the goal is to estimate mean population size for the area studied.

Boulanger and McLellan (2001) suggested closure correction factors of 17–25% over naïve estimates for a grizzly bear population in the Prophet River area of the Northern Rocky Mountains. Sampling methods were similar to the methods used here and the study area also included mountainous and boreal plains habitat (Poole et al. 2001). Boulanger and McLellan (2001) extrapolated a population estimate from bears whose mean capture distance was >10 km from the boundary to estimate density for the entire study area. This distance would exclude all bears along the boundary whose home range was <314 km², which seems overly conservative when compared to the home ranges observed on this study area, especially for bears living in the mountains (Ciarnello et al. 2001). Poole et al. (2001) demonstrated that the majority of the bears in the study area resided in the mountains; however, the centre of the study area was in the boreal plains (Fig. 10). Capture probabilities were lower on the boreal plains, which likely explains why Boulanger and McLellan (2001:Figs. 1 & 3) found a reduction in fidelity and capture probabilities at large distances from the edge. At about 20 km from the edge plateau bears become the majority in the sample and at 25 km from the edge, only 1 mountain bear remains in the sample (Fig. 10). This example demonstrates the sensitivity of the core correction technique to variation in the distribution and capture probabilities of individuals in the sample.

In all analyses we attempted to calculate separate closure corrections for each sex because we expected less closure bias for females because they have much smaller home ranges. Closure bias generally influenced female estimates closer to the boundary (Fig. 6, except for female black bears on the plateau), although the differences were often subtle. The reduction in sample size that results from dividing and excluding samples reduces power and can lead to spurious results. The results of the 3 smallest samples of the 6 presented are difficult to explain (Figs. 6a, c, e). Heterogeneity models are more sensitive to sample size than simple time models (Otis et al. 1978, Manning et al. 1995, Kendall 1999), and great care must be taken when using the core correction method with heterogeneity models. The jackknife model in particular tends to be biased low when recaptures are few (Otis et al. 1978). Sequentially reducing sample size could yield reduced estimates due to model bias that could be mistaken for closure bias. The core population correction method appears to be a more accurate method to correct for closure than the boundary strip method, but its application will be limited by sample size, as is the case for the similar nested grid method (Otis et al. 1978). The radiotelemetry method can also provide accurate estimates of density but a large and representative sample of collared bears must be collared during the study (Eberhardt 1990, Garshelis 1992). This is difficult not only because collaring is expensive but also because capture effort and success are rarely random with respect to the residency of bears.



Figure 10. Five-kilometre strips from the study area boundary for the Prophet River grizzly bear DNA inventory (Poole et al. 2001). Sites that detected grizzly bears are shown in solid circles, sites that did not detect grizzly bears are shown in open circles.

DNA-based inventory methods for bears

The high frequency and duration of rain during much of this study likely reduced both the capture success and the number of hair samples collected. Rain probably dilutes the effectiveness of the lure and knocks hair from the barbed wire to the ground. In addition to increasing search effort for hair on the ground and in the bait pile, the field crews also used spruce bows and moss to cover over bait piles once the blood and fish oil were applied. We hoped this would keep the lure drier, thus increasing capture probabilities. We demonstrate that bears can be detected along salmon streams in the interior of British Columbia using non-baited trails sets. S. Himmer (personal communication) and Davis (1998) have both used trail sets along salmon to sample coastal bears.

We deviated somewhat from hair sorting methods followed during previous inventories (Woods et al. 1999, Mowat and Strobeck 2000, Poole et al. 2001) due to logistic constraints and in order to test new ideas. Both technicians sorted bear hair into 3 groups: grizzly, black, and unknown, although 1 technician used the unknown category more often than the other. The technician that used the unknown category more often had slightly better success at identifying grizzly hair samples. Use of the unknown category saves little in laboratory costs because both grizzly and unknown samples are sent to the lab for species testing. However, the detection data for sites for which no sample is species tested, or all testing fails, is more accurate. This is especially important if the researcher intends to use the presence or absence of a bear species at each site to investigate habitat relationships. There are often a small number of sites for which all genetic analysis fails and detection must rely on visual sorting.

We followed the example of Boulanger and Himmer (2000) and labelled the group and proximity of each sample along the barbed wire. This allowed us to more objectively remove redundant samples. Although we did not test for the number of bears we missed, we genotyped 1,050 of 2,563 samples which were visually classified as grizzly bear or unknown, and were able to identify 326 captures of 239 grizzly bears. Our genetic analysis was less than half the cost of genotyping all the grizzly bear hair samples collected.

Considerable time can be saved by putting entire samples of underfur into extraction vials because these fine hairs are tedious to cut roots from. This project, and work by Mowat and Paetkau (2001) on marten (Martes americana) hair, confirmed that adequate template DNA to do multi-locus genotyping can be extracted from entire underfur. We also demonstrated that genotyping success is related to the number of roots put into an extraction. This relationship is intuitive because greater template DNA should increase genotyping success, as has been demonstrated for marmots (Marmota marmota; Gossens et al. 1998), bears (Boulanger 1998b, Mowat et al. 2000), and marten (Mowat and Paetkau 2001). We support the suggestion by Gossens et al. (1998) that 10 hairs be used when analysing single tubes from each sample. Taberlet et al. (1996) suggested conducting multiple analyses of samples with fewer hairs, but this approach is not practical in many field inventory situations because of the added cost; our error-checking results suggest that it is not necessary. Our regressions suggest that genotyping success can be improved by putting >10 guard hairs and >30 underfur in an extraction (Figs. 3 and 4). However, we had few samples with large numbers of hairs such as this and the relationship should be confirmed for large numbers of hairs. The number and type of hair is not the only variable affecting genotyping success because the regressions we developed were only able to correctly classify approximately 60% of the genotyping events. Other variables also affect genotyping success.

It appears that a large number of bears could be sampled with relatively small effort along salmon streams in the interior. Davis (1998) sampled black bears along British Columbia's mid-coast using barbed wire trail sets, although she baited her trails sets with salmon carcasses. S. Himmer (personal communication) sampled grizzly bears in Owikeno Inlet using trails along salmon streams, and we followed his advice in setting out sites. Himmer found that capture success of bears was high when trapping along salmon streams, and that bait was not necessary in achieving captures. Perhaps bear inventories can be done efficiently by trapping along salmon streams when the salmon are running, but it will be difficult to measure the residency of bears and hence calculate density.

MANAGEMENT RECOMMENDATIONS

Because DNA survey methods are so expensive, there will likely always be some need to use habitat-based extrapolations, like the Fuhr-Demarchi method, to predict bear abundance across broad areas. However, at present the Fuhr-Demarchi technique is so subjective that different individuals can come up with widely differing results for the same area. Thus, there is a need to modify the method so that it is objective, repeatable and testable. In the short-term, we suggest that managers should use DNAderived population estimates in various regions as benchmarks to calibrate the Fuhr-Demarchi method. The use of empirical methods to extrapolate abundance based on habitat analysis of survey data should also be considered (Boyce and MacDonald 1999) although tight-fitting statistical models often do not work well when applied to other areas. We suggest that until direct field density estimates are available for other areas in the Wildlife Management Region 7A, the Parsnip plateau density be considered representative of the surrounding plateau SBS forests in Wildlife Management Units 7-08–7-16 and 7-24– 7-26, and the mountain density be considered representative of the ESSF and Spruce-Willow-Birch (SWB) forests and alpine tundra on the adjacent west slopes of the Rocky Mountains in Wildlife Management Units 7-01–7-03, 7-17, 7-18, 7-23, 7-30, 7-37 and 7-41. Current harvest levels are only sustainable in the Hart Ranges hence harvests should be decreased in the 3 other study areas we worked in.

Salmon appear to be an important food source for grizzly bears in the upper Fraser River basin region, as demonstrated by the long distance movements of bears to salmon streams. The extremely low detection rate of black bears along the salmon streams suggests this resource may be not be shared among all bears, at least when salmon are few. Jacoby et al. (1999) found that black bears on the Pacific coast fed heavily on salmon when grizzly bears were rare but not when grizzlies were abundant. Consideration should be given to retaining access to all salmon streams for bears during resource planning. The affects of human disturbance may also require consideration and mitigation.

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LITERATURE CITED

- Austin, M.A. No date. A guide to the British Columbia Wildlife Branch step-down models for calculating population estimates for grizzly bears using the Fuhr-Demarchi method. Unpublished manuscript.
- Boulanger, J. 1998b. The effects of sampling factors on DNA viability in hair samples. Unpublished final report for B.C. Ministry of Environment, Lands and Parks, Victoria, BC.
- Boulanger J. 2001a. Analysis of the Elk Valley and Flathead valley DNA mark-recapture grizzly bear inventory projects. Final Report for B.C. Ministry of Environment, Lands and Parks, Cranbrook, BC.
- Boulanger J. 2001b. Estimates of the grizzly bear (*Ursus arctos*) population size using DNA based markrecapture, Upper Columbia River, British Columbia, Canada 1996-1998. Parks Canada, Revelstoke, BC.
- Boulanger, J., and C.J. Krebs. 1996. Robustness of capture-recapture estimators to sample biases in a cyclic snowshoe hare population. J. Appl. Ecol 33:530-542.
- Boulanger, J., and S. Himmer. 2000. Kingcome (1997) DNA mark-recapture grizzly bear inventory project. Unpublished final report for BC Ministry of Environment, Lands and Parks, Victoria, BC.
- Boulanger J., and B. McLellan. 2001. Closure violation bias in DNA based mark-recapture population estimates of grizzly bears. Canadian Journal of Zoology 79:642-651.
- Boutin, S. 1984. Home range size and methods of estimating snowshoe hare densities. Acta. Zool. Fennica. 171:275-278.
- Boyce, M.S. and L.L., McDonald. 1999. Relating populations to habitats using resource selection functions. Trends in Ecology and Evolution 14:268–272.
- Ciarniello, L.M., M.S. Boyce, D.R. Seip and D.C. Heard. In press. Grizzly bear habitat selection in mountain and plateau landscapes along the Parsnip River, British Columbia. International Conference on Bear Research and Management.
- Ciarniello, L.M., J. Paczkowski, D. Heard, I. Ross, and D. Seip. 2001. Parsnip grizzly bear population and habitat project, 2000 progress report. Unpublished report for Canadian Forest Products Ltd., Chetwynd, BC.
- Davis, H. 1998. Genetics of Kermode bears 1998: hair sampling. Progress Report for Western Forest Products, Vancouver, BC.
- Demarchi, D.A., R.D. Marsh, A.P. Harcombe and E.C. Lea. 1990. The Environment. Pages 55-144. *In* R.W. Campbell, N.K. Dawe, I. McTaggart-Cowan, J.M. Cooper, G.W. Kaiser and M.C.E. McNall, editors. The Birds of British Columbia. Volume 1. Royal British Columbia Museum. Victoria, BC. 514 pp.
- Dice, L. R. 1938. Some census methods for mammals. Journal of Wildlife Management 2:119-130.
- Eastern Slopes Grizzly Bear Project. 1998. Grizzly bear population and habitat status in Kanaskis Country, Alberta: A report to the Department of Environmental Protection, Natural Resources Service, Alberta. Eastern Slopes Grizzly Bear Project, University of Calgary, Calgary, AB. 91 pp.
- Eberhardt, L. L. 1990. Using radio-telemetry for mark-recapture studies with edge effect. Journal of Applied Ecology 27:259-271.
- Ennis, S, and T.F. Gallagher. 1994. PCR based sex determination assay in cattle based on the bovine Amelogenin Locus. Animal Genetics 25:425-427.
- Fuhr, B., and D.A. Demarchi. 1990. A methodology for grizzly bear habitat assessment in British Columbia. B.C. Ministry of Environment, Wildlife Bulletin No. B-67, Victoria, BC.

- Garshelis, D.L. 1992. Mark-recapture density estimation for animals with large home ranges. in D. R. McCullough and R. H. Barrett eds. Wildlife 2001: populations. Elsevier Press Science, London.
- Gibeau, M.L., S. Herrero, J.L Kansas, and B. Benn. 1996. Grizzly bear population and habitat status in Banff National Park. A report to the Bow Valley Task Force. Eastern Slopes Grizzly Bear Project, University of Calgary, Calgary, AB. 62 pp.
- Gossens, B., L.P. Waits, and P.T. Taberlet. 1998. Plucked hair samples as a source of DNA: reliability of dinucleotide microsatellite genotyping. Molecular Ecology 7:1237-1241.
- Hamer, D., and S. Herrero. 1987. Grizzly bear food and habitat in the Front Ranges of Banff National Park, Alberta. International Conference on Bear Research and Management 7:199-214.
- Hamer, D., S. Herrero, K. Brady. 1991. Food and habitat used by grizzly bears along the continental divide in Waterton Lakes National Park, Alberta. Canadian Field Naturalist 105(3):325-9.
- Hilderbrand, G.V., C.C. Schwartz, C.T. Robbins, M.E. Jacoby, T.A. Hanley, S.M. Arthur, and C. Servheen. 1999. The importance of meat, particularly salmon, to body size, population productivity, and conservation of North American brown bears. Canadian Journal of Zoology 77:132-138.
- Jacoby, M.E., G.V. Hilderbrand, C. Servheen, C.C. Schwartz, S.M. Arthur, T.A. Hanley, C.T. Robbins, and R. Michener. 1999. Trophic relations of brown and black bears in several western North American ecosystems. Journal of Wildlife Management 63:921-929.
- Kendall, W.L. 1999. Robustness of closed capture-recapture methods to violations of the closure assumption. Ecology 80:2517-2525.
- Kenward, R.E., V. Marcström, and M. Karlbom. 1981. Goshawk winter ecology in Swedish pheasant habitats. Journal of Wildlife Management 45:397-408.
- Kolenosky, G.B. and S.M. Strathearn. 1987. Black bear. Pages 443-454 *in* M. Novak, J.A. Baker, M.E. Obbard, and B. Malloch, editors. Wild furbearer management and conservation in North America. Ontario Trappers Association, North Bay, ON.
- Johnson, M., and K.C. Kendall. 2001. Effectiveness of liquid scent lures for Brown Bears. Ursus: In Press.
- LeFranc, M.N., M.B. Moss, K.A. Patnode, and W.C. Sugg, editors. 1987. Grizzly bear compendium. Interagency Grizzly Bear Committee, Washington, DC, USA.
- McLellan, B.N. 1994. Density-dependent population regulation of brown bears. Pp15-24. *In* M. Taylor, editor. Density-dependent population regulation of black, brown, and polar bears. International Conference on Bear Research and Management. Monogr. Series No.3. 43pp.
- McLellan, B.N. 1989. Dynamics of a grizzly bear population during a period of industrial resource extraction. I. Density and age-sex composition. Canadian Journal of Zoology 67:1856-1860.
- McLellan, B.N., and F.W. Hovey. 2001. Habitats selected by grizzly bears in a multiple use landscape. Journal of Wildlife Management 65:92-99.
- McLellan, B.N., F.W. Hovey, R.D. Mace, J.G. Woods, D.W. Carney, M.L. Gibeau, W.L. Wakkinen, and W.F. Kasworm. 1999. Rates and causes of mortality of grizzly bears in the interior mountains of British Columbia, Alberta, Montana, Washington, and Idaho. Journal of Wildlife Management 63:911-920.
- Mace, R.D., and J.S. Waller. 1998. Demography and population trend of grizzly bears in the Swan Mountains, Montana. Conservation Biology 12:1005-1016.
- Mace, R.D., and J.S. Waller. 1997. Final report: grizzly bear ecology in the Swan Mountains, Montana. Montana Fish, Wildlife and Parks, Helena, Montana, USA.

- Mace, R.D., S.C. Minta, T.L. Manley, and K.E. Aune. 1994. Estimating grizzly bear population size using camera sightings. Wildlife Society Bulletin 22:74-83.
- MacHutchon A.G., S. Himmer, and C.A. Byrden 1993. Khutzeymateen Valley grizzly bear study: Final Report. Victoria BC: Ministry of Environment, Lands, and Parks, Victoria, BC. Report no. R-25.
- Manning, T., W.D. Edge, and J.O. Wolff. 1995. Evaluating population-size estimators: an empirical approach. Journal of Mammalogy 76:1149-1158.
- Martinka, C.J. 1974. Population characteristics of grizzly bears in Glacier National Park, Montana. Journal of Mammalogy 55:21-29.
- Meidinger, D., and J. Pojar, editors. 1991: Ecosystems of British Columbia. Special Report Series 6, B.C. Ministry of Forests, Research Branch, Victoria, BC.
- Miller, S.D. 1990. Population management of bears in North America. International Conference on Bear Research and Management 8:357-373.
- Miller, S.D., G.C. White, R.A. Sellers, H.V. Reynolds, J.W. Schoen K. Titus, V.G., Jr. Barnes, R.B. Smith, R.R. Nelson, W.B. Ballard and C.C. Schwartz. 1997. Brown and black bear density estimation in Alaska using radiotelemetry and replicated mark-resight techniques. - Wildlife Monograph 133:1-55.
- Ministry of Environment, Lands and Parks. 1999. Grizzly bear harvest management. Procedure Manual. Volume 4 Section 7 Subsection 04.04.
- Mowat, G., and C. Strobeck. 2000. Estimating population size of grizzly bears using hair capture, DNA profiling, and mark-recapture analysis. Journal of Wildlife Management 64:183-193.
- Mowat, G., K. Stalker, G. Stenhouse, and C. Strobeck. 2000. Foothills model forest grizzly bear inventory 1999. Final Report, Foothills Model Forest, Hinton, AB.
- Mowat, G., and D. Paetkau. 2001. Estimating marten population size using hair capture and genetic tagging in southeast British Columbia. Final report prepared for Slocan Forest Products, Slocan, B.C., and B.C. Environment, Lands and Parks, Nelson, BC.
- Nagy, J.A.S., and M.A. Haroldson. 1989. Comparisons of some home range and population parameters among 4 grizzly bear populations in Canada. International Conference on Bear Research and Management 8:227-235.
- Nagy, J.R., and J.R. Gunson. 1990. Management plan for grizzly bears on Alberta. Wildlife Management Planning Series Number 2, Alberta Forestry, Lands and Wildlife, Fish and Wildlife Division, Edmonton, AB.
- Otis, D.L., K.P. Burnham, G.C. White, and D.P. Andersen. 1978. Statistical inference from capture data on closed animal populations. Wildlife Monographs 62:1-135.
- Paetkau, D.W., and C. Strobeck. 1996. Mitochondrial DNA and the phylogeography of Newfoundland black bears. Canadian Journal of Zoology 74:192-196.
- Paetkau, D.W., G.F. Shields, and C. Strobeck. 1998. Gene flow between insular, coastal and interior populations of brown bears in Alaska. Molecular Ecology 7:1283-1292.
- Pelton, M.R. 1983. Black Bears. Pages 504-514 in J. A. Chapman and G. A. Feldhammer eds. Wild mammals of North America: biology, management, economics. John Hopkins University Press, Baltimore, MD. USA.
- Poole, K.G., G. Mowat, and D.A. Fear. 2001. DNA-based population estimate for grizzly bears in northeastern British Columbia, Canada. Wildlife Biology 7:65-75.

- Poole, K.G., G. Mowat, and D. Pritchard. 1999. Using GPS and GIS for navigation and mark-recapture for sightability correction in moose inventories. Alces 35:1-10.
- Proctor, M.F., B.N. McLellan, and C. Strobeck. 2002: Population fragmentation of grizzly bears in southeastern British Columbia, Canada. Ursus 13:153-160.
- Reynolds, G. 1989. Climatic data summaries for the biogeoclimatic zones of British Columbia. B.C. Ministry of Forests, Research Branch. Victoria, BC. Unpublished report.
- Russell, R.H., J.W. Nolan, N.G. Nagy, and G.H. Anderson. 1979. A study of the grizzly bear in Jasper National Park 1975 to 1978 final report. Canadian Wildlife Service, Edmonton, AB.
- Simpson, K., K.B. Hebert, and G.P. Woods. 1985. Habitats and management of the grizzly bear in the Columbia mountains of British Columbia. Unpublished Report for B.C. Ministry of Environment, Nelson, BC.
- Smallwood, K.S., and C. Schonewald. 1996. Scaling population density and spatial pattern for terrestrial, mammalian carnivores. Oecologia 105:329-335.
- Strom, K., M. Proctor, and J. Boulanger. 1999. Grizzly bear population survey in the central Purcell Mountains, British Columbia. Final report for B.C. Environmental Assessment Office, Victoria, BC.
- Taberlet, P., S. Griffin, B. Goossens, S. Questiau, V. Manceau, N. Escaravage, L. P. Waits, and J. Bouvet. 1996. Reliable genotyping of samples with very low DNA quantities using PCR. Nucleic Acids Research 24: 3189-3194.
- Taberlet, P., J.-J. Camarra, S. Griffin, E. Uhres, O. Hanotte, L.P. Waits, C. Dubois-Paganon, T. Burke and J. Bouvet. 1997. Noninvasive genetic tracking of the endangered Pyrenean brown bear population. Molecular Ecology 6:869-876.
- Taylor, M., editor. 1994. Density-dependent population regulation of black, brown, and polar bears. International Conference on Bear Research and Management. Monograph Series No. 3. 43pp.
- Waller, J.S., and R.D. Mace. 1997. Grizzly bear habitat selection in the Swan Mountains, Montana. Journal of Wildlife Management 64:1032-1040.
- Wielgus, R.B., and F.L. Bunnell. 1994. Dynamics of a small, hunted brown bear population in southwestern Alberta, Canada. Biological Conservation 67:161-166.
- Wielgus, R.B., F.L. Bunnell, W.L. Wakkinen, and P.E. Zager. 1994. Population dynamics of Selkirk mountain grizzly bears. Journal of Wildlife Management 58:266-272.
- White, G.C., D.R. Andersen, K.P. Burnham, and D.L. Otis. 1982. Capture-recapture and removal methods for sampling closed populations. Los Alamos Nat. Laboratory LA-8787-NERP.
- White, G.C. and K.P. Burnham. 1999. Program MARK: Survival estimation from populations of marked animals. Bird Study 46 Supplement, 120-138.
- Woods, J.G., D. Paetkau, D. Lewis, B.N. McLellan, M. Proctor, and C. Strobeck. 1999. Genetic tagging free ranging black and brown bears. Wildlife Society Bulletin 27:616-627.